INVITED REVIEWS AND META-ANALYSES

The impact of global climate change on genetic diversity within populations and species

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Abstract
Genetic diversity provides the basic substrate for evolution, yet few studies assess the impacts of global climate change (GCC) on intraspecific genetic variation. In this review, we highlight the importance of incorporating neutral and non-neutral genetic diversity when assessing the impacts of GCC, for example, in studies that aim to predict the future distribution and fate of a species or ecological community. Specifically, we address the following questions: Why study the effects of GCC on intraspecific genetic diversity? How does GCC affect genetic diversity? How is the effect of GCC on genetic diversity currently studied? Where is potential for future research? For each of these questions, we provide a general background and highlight case studies across the animal, plant and microbial kingdoms. We further discuss how cryptic diversity can affect GCC assessments, how genetic diversity can be integrated into studies that aim to predict species' responses on GCC and how conservation efforts related to GCC can incorporate and profit from inclusion of genetic diversity assessments. We argue that studying the fate of intraspecific genetic diversity is an indispensable and logical venture if we are to fully understand the consequences of GCC on biodiversity on all levels.

Keywords: cryptic species, global change biology, phylogeography, species distribution modelling, species range projections

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Introduction
Intraspecific genetic variation provides the basis for any evolutionary change and is thus the most fundamental level of biodiversity (May 1994). In the light of current global climate change (GCC), it is necessary to study the effects of climatic alterations on intraspecific genetic diversity if we are to fully understand the evolutionary consequences of GCC and its long-term effects on biodiversity. However, despite an increasing number of studies examining the effects of GCC on biodiversity on species and community level, few studies focus on patterns of intraspecific genetic variation.

Global climate change will impact intraspecific genetic diversity in many ways. These include, but are not limited to (i) changes in the distribution of genetic variants in space and time as the ranges of populations and species change, (ii) changes in levels of phenotypic plasticity of individuals and populations as they respond to new environmental conditions, as well as (iii) evolutionary adaptation to changing environmental conditions (Hoffmann & Sgrò 2011). In many cases, these changes will reduce genetic diversity in populations and species, in extreme situations to the point where genetic impoverishment will contribute to reduced population viability and extinction.

In the following review, we first address the question why the impact of GCC on genetic diversity merits
scientific scrutiny. Here, we briefly outline the importance of genetic diversity for species reactions to GCC, provide examples of the effects of GCC on commercially valuable organisms where our basic understanding in the field is grounded, and raise the issue of cryptic diversity in the context of GCC. Second, we ask how GCC impacts intraspecific genetic diversity. In this section, we assess the importance of GCC-induced range shifts and GCC effects on the selection regime for genetic diversity. Third, we ask how scientists are currently assessing the impact of GCC on intraspecific genetic diversity and the issues they are facing. We address the question what we can learn from inferences about a species’ history and from assessments of neutral and non-neutral genetic diversity and its interactions with the environment. Finally, we outline how we think this line of research will proceed in the future. We highlight genetic diversity as an important but previously largely neglected level of biodiversity that is fundamental for species adaptive capacities. We aim to raise awareness for this shortcoming and encourage the global change biology community to embrace and further the knowledge on the impacts that GCC will have on biodiversity’s most fundamental level.

For the purpose of this review, we define genetic diversity as all the genetic variants within and among populations of evolutionary lineages, where evolutionary lineages can represent recognized morphospecies, morphologically cryptic species or other evolutionary significant units (ESUs).

Why study the effects of GCC on intraspecific genetic diversity?

Species can react to GCC by persisting in new conditions through ecological plasticity or adaptation (Riddle et al. 2008; Scoble & Lowe 2010; Hoffmann & Sgrò 2011) or they can avoid new conditions by shifting their habitat or their range (Parmesan et al. 1999; Chen et al. 2011). Failure to succeed in either of these mechanisms will likely lead to population extirpation or—in the worst case—extinction of entire species (Dawson et al. 2011). However, no matter which of the mentioned trajectories an individual population or species will take under GCC, all will influence the amount and distribution of intraspecific genetic diversity, most often associated with a loss of genetic variation. Genetic variants with phenotypic effect are, however, the fundamental basis for evolutionary change and ultimately for biodiversity as such. Genetic diversity has been shown to be important for the fitness of individuals as high levels of heterozygosity may increase individual fitness because the effect of deleterious mutations can be counterbalanced (Chapman et al. 2009). Also, the stress resistance of populations (Nowak et al. 2007; Markert et al. 2010) and their adaptive potential (Frankham 2005) is positively associated with the degree of overall genetic diversity, the loss of which is therefore potentially a threat to the affected population or species.

The potential of GCC to reduce intraspecific genetic diversity does not only have academic or conservation consequences but pertains to the sustenance of humanity. In general, genetic diversity has been recognized to be important for maintaining ecosystem services, for example, by ‘reducing pest and disease problems, and encouraging recovery from disturbance (Burton et al. 1992)’. It is not by chance that most work examining the effects of GCC on genetic diversity has focussed on crops (e.g. rice, Negrao et al. 2008), commercially important fish (e.g. salmonids, Bryant 2009), forest trees (e.g. Parker et al. 2000) or more generally on agricultural systems (Challinor et al. 2009). In crop sciences, it is now recognized that by focussing on specialized breed lines, the potential of crops to adapt to GCC is limited and that biosynthetic pathways are likely to be lost, limiting the potential nutrient value of crop plants (Reynolds & Borlaug 2006; Burlingame et al. 2009). In response to these threats, ideas have begun circulating to inbreed old cultivars (e.g. Charmet 2011) to maintain and preserve landraces for sustaining adaptive potential in agricultural resources (Newton et al. 2010), in an effort termed the ‘doubly green revolution’ (Reynolds & Borlaug 2006). These approaches have also been adapted in the forest industry: Aravanopoulos (2010) proposes using Mediterranean stocks of fast-growing, economically sought tree species to genetically diversify northern forests with tree clones that were selected under higher temperature or drier conditions. The impact of GCC on agriculturally important species is likely to be exacerbated by inbreeding due to human harvesting (Cibrian-Jaramillo et al. 2009). Increased anthropogenic fragmentation of populations of both economically important and other species that limits gene flow may also leave populations that are locally adapted to current conditions, but maladapted to future conditions under GCC, at peril of increased stress (Davis & Shaw 2001; Jump & Penuelas 2005; Hof et al. 2011a).

Ongoing GCC also impacts the genetic diversity of species that are not studied nearly as well as most economically relevant organisms. For these species, an additional issue arises from the fact that taxonomically recognized morphospecies are often not the evolutionary, ecologically or even economically relevant units. The ubiquitous presence of cryptic species or ESUs (Pfenninger & Schweng 2007) suggests that morphospecies-based approaches may seriously underestimate GCC effects on biodiversity (see Box 1). In a recent study, for example, Bálint et al. (2011) showed that without acknowledging...
intraspecific genetic variation and cryptic diversity, GCC effects are likely to be drastically underestimated. Despite the obvious shortcomings of morphospecies level assessments, subspecific genetic diversity has not yet received much of its deserved attention in the biodiversity and climate change discussion (e.g. Bellard et al. 2012).

**Box 1 How does cryptic diversity affect GCC projections?**
Cryptic diversity is a common phenomenon and has become a focus of biodiversity research following (i) methodological advances in integrated taxonomy (Wheeler 2004, 2008; Dayrat 2005; Padial et al. 2010), DNA taxonomy (Vogler & Monaghan 2007), DNA barcoding (Hebert et al. 2003) and (ii) a general increase in biodiversity studies that apply molecular tools. In particular, widespread species with broader ecological niches are often taxonomically complex entities that represent numerous subspecies or other cryptic diversity units (Callaghan et al. 2004; Ujvárosi et al. 2010). Cryptic diversity may complicate assessments of GCC effects on biodiversity in a number of ways. First, cryptic species or cryptic lineages can follow independent evolutionary trajectories, that is, they represent independent ESUs and may thus show different responses to GCC (Davis & Shaw 2001; Galbreath et al. 2010; Heurertz et al. 2010). In addition, taxa that in the past evolved high levels of genetic diversity or multiple ESUs associated with varying environmental conditions may be more likely to do this again in the future (Callaghan et al. 2004). However, the rate of ongoing GCC may be quicker than major historic environmental changes, and this limits the amount of time for evolutionary responses (but see Steffensen et al. 2008 and Hof et al. 2011b). Additional anthropogenic pressures like habitat fragmentation may further impact species responses. Nonetheless, the fate of independent cryptic lineages or ESUs can vary under different GCC scenarios (Bálint et al. 2011; Habel et al. 2011) and may be very different from the assessment for a morphospecies as a whole (Bálint et al. 2011; Taubmann et al. 2011; Fig. 1).

Second, cryptic diversity complicates palaeo-reconstructions: cryptic species with different ecological niches or environmental change responses are necessarily considered as one unit in these reconstructions (Bauch et al. 2003). This will compromise the use of palaeontological data to infer historic reactions to environmental change and the use of these inferences to inform future predictions on GCC responses. Ancient DNA approaches may provide a solution for identifying cryptic diversity with the palaeorecords of select taxa (Magyari et al. 2011).

Third, due to the omnipresence of cryptic diversity and the individualistic responses of ESUs to environmental change, community diversity comparisons and assessments based on morphospecies are oversimplified and may even lead to inefficient conservation practices (Fayle et al. 2011; see Box 2). Because cryptic species and cryptic lineages are more or less evenly distributed among major metazoan taxa and biogeographical regions (Pfenninger & Schwenk 2007), these difficulties should generally be taken into account in studies aiming at assessing GCC effects on species or communities. Several different analytical tools and approaches facilitate assessments of cryptic diversity within a given sample (e.g. Ratnasingham & Hebert 2007; Monaghan et al. 2009). Expanding on the approach used in Bálint et al. (2011), Pfenninger et al. (2012) suggest a methodological approach to make GCC inferences based on ESUs that assess the adequacy of sampling depth at different organizational levels of intraspecific genetic diversity (haplotypes, ESUs, species; see Box 3).

**How does GCC affect genetic diversity?**
We extracted two fundamental but not mutually exclusive processes by which GCC may affect genetic diversity: (i) change in the geographical location and extent of the range and (ii) changes in the local selection regime. Both processes are predicted to have specific effects on the genetic make-up, which we will address in turn.

**Genetic consequences of range shifts**
Effects at the edge of ranges. Range shifts are usually the combined effect of the colonization of newly emerging suitable habitat coinciding with the migration and then extinction in areas that have become unsuitable. The effects of range shifts on neutral genetic diversity have recently been subject of numerous simulation studies that advanced our understanding on how these parameters influence the temporal and spatial patterns of neutral genetic diversity under range shift scenarios. Cobben et al. (2011), McInerny et al. (2009) and Arenas et al. (2012) show that the leading edge of a shifting range under GCC has low levels of neutral genetic diversity. This is caused by recurring founder effects, allele surfing and because only a part of the original genetic variation moves to a newly colonized habitat. While the leading edge of a shifting population often comprises low levels of genetic variation, McInerny et al. (2009) show that the leading edge is also the source for most of the surviving lineages and persisting alleles,
1, 3, 7, 15, 19 individuals

Median vector

Extant/persisting and lost GMYC species

Extant/persisting and lost mtCOI haplotype, color-coded by region

Connection among extent/persisting and lost haplotypes/median vectors

color-coding of regions:

Sampling site

Projection of climatically suitable areas:

- Current
- 2080 under B2a Scenario
- 2080 under A2a Scenario
while trailing edge lineages and alleles are more likely to go extinct. Under otherwise unchanged conditions, range contractions should lead to decreases in effective population size and in extreme cases to population bottlenecks that may reduce genetic diversity of populations (e.g. O’Brien et al. 1987; Hewitt 1996; Luikart et al. 1998). In a simulation study, Arenas et al. (2012) explicitly test the effects of range contractions under different models of dispersal directed either towards a potential refuge or equally in all directions. In their simulations, the speed of range contraction was very important. Somewhat counter-intuitively they show that slow-range contractions can lead to greater losses of overall genetic diversity than fast-range contractions. Under fast-range contractions, initial levels of genetic diversity are better preserved, because slower-range contractions are accompanied by more coalescence events and ultimately individuals sampled from the surviving refugia are more likely to share common ancestors.

Strong selection pressure may act on the leading edge of an expanding population, for example, on dispersal capacity or host selection in insects (Hill et al. 2011). In a selective sweep, newly advantageous alleles as well as the linked neutral alleles become fixed in the affected subpopulation, population or species, thus reducing local genetic diversity. Another process by which local genetic drift can cause reduced genetic diversity in the leading edge of an expanding population is ‘surfing’ (reviewed by Excoffier & Ray 2008). Allele surfing defines the situation when an allele becomes over-proportionally frequent at the expanding front through genetic drift. The pattern resulting from this process may be indistinguishable from that of a selective sweep, although the underlying process without selection is vastly different and requires a different evolutionary interpretation (Excoffier et al. 2009). In a rare empirical study on allele surfing, Hallatschek et al. (2007) use two fluorescently marked strains of *Escherishia coli* (Migula 1895) to demonstrate that surfing leads to severe changes in the neutral variation of natural populations. Genetic population structure also changed because individual alleles dominated certain regions of newly invaded territory, without these alleles being under selection. It appears that range expansion may lead to complex patterns of population genetic structure with regions of low genetic diversity separated by sharp gradients in allele frequency of individual loci and that these patterns can arise without the influence of rare long-distance dispersal events. However, this structure is likely to erode over time due to gene flow between contact zones of different adjacent regions (Excoffier & Ray 2008).

These theoretically derived predictions have important consequences for expectations of the genetic make-up of populations under GCC conditions if species respond through range shifts. First, all studies show that range shifts should lead to reduced overall genetic variation. Second, rear-edge populations of species postglacially recolonizing central and northern Europe from southern refugia have been shown to harbour large proportions of genetic diversity and ancestral lineages. Thus, these rear-edge populations play an important role in maintaining long-term genetic diversity in these species (Hampe & Petit 2005). Based on the simulation studies, these lineages appear particularly threatened and may deserve particular attention in conservation (see Box 2).

**Effects within the range.** Besides the location of a (sub) population within a shifting range (leading edge, centre or rear-edge), simulation studies conclude that neutral genetic diversity of populations decreases with increased short-term regional climate variation (Cobben et al. 2011) and with increasing speed of the range shift (Arenas et al. 2012). Some recent empirical studies have used simple models to project losses of genetic diversity associated with range shifts (Sork et al. 2010; Bálint et al. 2011; Collevatti et al. 2011; Habel et al. 2011; Taubmann et al. 2011; Alsos et al. 2012). While these are pioneering studies in addressing the effects of GCC on the distribution and projected losses of intraspecific genetic variation, they suffer from relatively simple dispersal models, do not account for adaptation and have with the exception of Sork et al. (2010) not implemented measures of short-term regional climate variation. Empirical studies on population structure also made inferences on the effects of range shifts on the distribution of genetic diversity (Campos et al. 2010; Pfenninger et al. 2011;)

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**Fig. 1** Schematic figure of projected genetic diversity losses of the caddisfly *Drussa discolor*. Shown is the mtCOI haplotype diversity from the range-wide sampling of *D. discolor* in the median joining network (left column). Coloured circles represent haplotypes; colour coding indicates regional origin of the specimen carrying a specific haplotype; and haplotype diameter is scaled to the number of individuals carrying a specific haplotype. Lines between haplotypes indicate connections; connections are not scaled to genetic distance; and median vectors connect lineages. Species delimited using a general mixed Yule coalescent model (GMYC species, Monaghan et al. 2009) are grouped by shaded shapes. Grey shapes indicate current or persisting GMYC species; orange shapes indicate GMYC species projected to be lost under the respective IPCC CO$_2$ emissions scenario. The right column shows models of the climatically suitable areas for *D. discolor* in the present (top) and 2080 under the B2a CO$_2$ emissions scenario (middle) and A2a CO$_2$ emissions scenario (bottom). White circles show localities used to derive the climatically suitable areas and haplotype distribution. Data from Pauls et al. 2006 and Bálint et al. 2011.
GCC responses will vary in different parts of the species range. Yang et al. (2011) observed shifts in intraspecific genetic diversity within an alpine chipmunks’ unchanged range, highlighting the fact that interpretations of observed spatial migration at the species level may not account for more subtle subspecific GCC responses. Following up this work, Rubidge et al. (2012) show how GCC-induced range reductions of one alpine chipmunk species in California resulted in patterns of genetic erosion through time, while a congeneric species showed no signs of range reduction, range shift or genetic erosion.

Box 2 Conservation of genetic diversity under global climate change

Technical advances in the field of molecular genetics along with the rising importance and public awareness of nature conservation issues have led to the rise of ‘conservation genetics’ over the past two decades (e.g. DeSalle & Amato 2004). Examples for the successful application of molecular markers in conservation research and population management are manifold and include the estimation of genetic diversity loss and grades of inbreeding (e.g. Marsden et al. 2012), correct species assignment (e.g. Rach et al. 2008), population monitoring (Schwartz et al. 2007), delineation of conservation units (Fraser & Bernatchez 2001), revealing introgression from domestic forms into wild populations (Randi 2008) and tracking the success of invasive species (e.g. Drungosch & Parker 2008) or re-introduced populations (e.g. De Barba et al. 2010). In a world of rapid environmental change, such as ongoing GCC, genetic diversity within and between populations undoubtedly becomes increasingly important, as it allows populations to adapt to environmental change and might enhance stress resistance of populations (see text for details). With this in mind, we suggest three areas where incorporation of genetic diversity measures in GCC-related species conservation strategies are particularly important:

1 Population management for critically endangered populations, for which genetic diversity loss and inbreeding might pose direct and severe concerns. The use of high-resolution marker sets covering large parts of the genome seems most appropriate for this purpose. Direct measures of inbreeding depression, however, do require experimental approaches, which are hardly ever applicable for the species of interest. The finding that inbreeding depression is enhanced under environmental stress (Armbruster & Reed 2005), including temperature stress, has particular relevance under GCC conditions and needs to be implemented in population viability analyses.

2 Assignment of populations and regions with particular conservation value under GCC species distribution models (SDM) are quite commonly used in conservation efforts to assess the potential of certain areas as reserves for target species or communities under GCC (e.g. Ponce-Reyes et al. 2012). Recent studies suggest using SDM alongside genetic assessments to project potential diversity losses under GCC (e.g. Scoble & Lowe 2010; Bálint et al. 2011; Habel et al. 2011; Taubmann et al. 2011; Alsom et al. 2012; Penninger et al. 2012). Combining these data will allow prioritizing populations and regions for conservation, allowing for an optimized balancing between future survival probabilities and preservation of evolutionary potential. This strategy requires sound measures of genetic diversity as suggested by Penninger et al. (2012) and will be most effective on large (area-wide) scales and among genetic lineages with independent evolutionary histories (e.g. ESUs).

3 Estimating dispersal capacities is not directly related to the conservation of genetic diversity itself. However, the ability to disperse is of crucial importance for organisms to track shifting climatic niches under GCC. Currently, the unknown dispersal abilities of species are considered one of the blind spots of current attempts to project GCC effects on biodiversity (Engler et al. 2009) and also limit conservation efforts more generally (Smith & Green 2005). The use of fine-scale genetic analyses, for example, by microsatellites or single nucleotide polymorphisms (SNP) panels and methodological approaches implemented in the emerging field of landscape genetics (Manel et al. 2003) promises to provide crucially needed data not only to identify dispersal events, but more importantly to reveal the extent of gene flow in time and space.

A way by which GCC and range shifts may enhance levels of genetic diversity apart from increasing overall mutation rate is the modification of reproductive isolation among lineages and species (Hoffmann & Sgrò 2011). Phylogeographic studies have provided ample evidence that postglacial climate shifts triggered expansions and
migrations that brought previously isolated lineages into secondary contact, thereby mutually increasing local genetic diversity (e.g. Hewitt 2000; Pfenninger & Posada 2002; Pauls et al. 2006, 2009). Disturbance regimes in general can lead to hybridization among isolated genetic lineages (Pfennig 2007; Schwenk et al. 2008), and postglacial secondary contact has also led to climate-driven hybridization events in several species. Hailer et al. (2012), for example, showed that polar bears (Ursus maritimus Phipps 1774) display high similarity to brown bears (Ursus arctos Linnaeus 1758) in mtDNA sequences, but not in nuclear genes. This is best explained by a ‘mitochondrial capture’ event of brown bear mtDNA during past phases of warm climates, which reduced the effective size of the polar bear population and facilitated introgression of genetic material. Similar patterns are known for other species as well, for example, hares (Melo-Ferreira et al. 2005) and butterflies (Zakharov et al. 2009). It was recently also shown that specific weather conditions were driving hybridization rates in two butterflies species (Janner et al. 2012), suggesting a great potential of GCC to modify species boundaries. Supporting evidence for increased introgression by hybridization under GCC conditions comes from the copepod Tigriopus californicus (Baker, 1912), where hybrid breakdown was less severe under thermal stress (Willett 2012). However, also the contrary was observed in parasitic wasps (Koevoets et al. 2012), stressing the idiosyncratic ways in which GCC will affect individual systems.

**Genetic consequences of GCC on the selection regime**

**Variaotions in micro-evolutionary responses.** Populations may face changing environmental conditions without directly responding through habitat or range shifts. Recent studies indicate that the genetic diversity of stationary populations may also be affected by GCC. A species’ ability to cope with changed conditions depends on the evolutionary adaptive capacity (Riddle et al. 2008) via micro-evolution, for example, selection for local genotypes better adapted to changing environmental conditions, but also including the evolution of pheno-typic plasticity (Canale & Henry 2010; Hoffmann & Sgrò 2011). Adaptive micro-evolutionary processes rely on sufficient genetic variation upon which natural selection can act (Hoffmann & Sgrò 2011) and the establishment probability of beneficial mutations (Peischel & Kirkpatrick 2012). Under a deteriorating environment, such as GCC represents for many species, adaptive micro-evolutionary processes will tend to reduce genetic variation at the selected loci and, more importantly, in those parts of the genome that are hitchhiking with it (Via & West 2008; Via 2009). As Charlesworth et al. (1997) could show, this hitchhiking process affects larger parts of the genome the smaller the population is. Therefore, fast increase in and multiple levels of environmental stress can strip a population of most of its genetic variability as it adapts to them, reducing the possibility to react to future selective challenges. A series of laboratory experiments on nonbiting midges suggested that exposure to a stressor over a few generations can indeed lower neutral genetic diversity by adaptation as well as enhanced genetic drift (Vogt et al. 2007; Nowak et al. 2009) and diminish the possibility to adapt to a secondary stressor (Vogt et al. 2010).

As does genetic variation, adaptation potential varies across a species’ populations and its range (Davis & Shaw 2001; Eckert et al. 2008). It is thus likely that individual populations within a species will react differently to GCC (e.g. Proccacini et al. 2007), especially if there are stronger selective pressures in different parts of the range or changes in selection pressure (Hoffmann & Sgrò 2011), for example, to stronger temperature changes in certain parts of a range (e.g. Jensen et al. 2008), to accelerated range expansion in leading edge populations (e.g. Hill et al. 2011), or to stronger competition through climate amelioration in the centre of the range of Arctic species (e.g. Callaghan et al. 2004). Good examples of this are many invasive species that adapt very rapidly to new selective pressures in the non-native ranges (Sax et al. 2007). Also, two recent studies have highlighted that different geographical accessions of the model species Arabidopsis thaliana (L.) Heynh. 1841 are locally adapted to climate conditions and show that relative fitness is linked to specific climate-adapted genetic loci (Fournier-Level et al. 2011; Hancock et al. 2011). Such differential adaptations to the same or different selective pressures may even foster reproductive isolation (Schluter 2001; Via 2012).

**The speed of ongoing GCC and effects of increased climate variation.** The speed of adaptation is an important component in GCC and is related to the strength of selective pressures on a population or species, the rate with which these selective pressures change and the adaptive potential of populations and species (Hoffmann & Sgrò 2011). Trees, for example, are rather long-lived in relation to the speed of current GCC. However, the high levels of genetic diversity and large effective population sizes of many tree species greatly increase their chances of adapting within a few generations (Petit & Hampe 2006). On the other hand, the current rate of GCC is so rapid—though not unprecedented in recent geologic history (Steffensen et al. 2008; Høi et al. 2011b; Tóth et al. 2011)—that the resulting strong selection pressures may rapidly distance populations from the environmental conditions to which they are locally adapted and promote local extirpation (Davis & Shaw 2001), even in
trees (Kramer et al. 2008). Even in cases of the recent geologic history when a forest is able to respond to rapid climate change with fast horizontal range shifts (e.g. Magyari et al. 2012), ancient DNA sequences connect plausible decreases in genetic diversity of a tree population to Holocene climatic oscillations (Magyari et al. 2011).

Most GCC-related research has focused on changes in climatic means, for example, warming temperature or general changes in annual precipitation. While changes in mean climate conditions are likely to cause losses in genetic diversity in many species, increases resulting from GCC are also plausible. Higher temperatures, for example, will generally increase metabolism in the majority of species, and this is linked with increased mutation rates (Muller 1928; Davis et al. 2005; Stegen et al. 2009; but see Held 2001). It remains unclear, however, if increased mutation rates could in turn add significantly to standing functional variability (Garcia et al. 2010; McGaughran & Holland 2010). Increased climate variation could also have major effect on genetic diversity, but its effects have rarely been studied. Increases in climate variation are expected for both precipitation patterns as well as temperature conditions (Karl et al. 1995; Christensen et al. 2007). Because any shift in selection regime is likely to change the frequency distribution of the responsive alleles in populations, both kinds of increases in short-term climactic variation have the potential to affect populations [e.g. changes in population growth rates (Drake 2005)] and individuals [e.g. changes in an individuals’ phenotypic plasticity-like intra-annual changes in individual growth rates (e.g. Nussey et al. 2005)].

In a rare empirical case study, Avolio et al. (2012) show that diversity in genotypes of a dominant prairie grass species declined significantly following 10 years of increased intra-annual variation in precipitation. While genotype diversity decreased, the authors observed decreases in genotype similarity within experimental plots, suggesting a local increase in genetic diversity. Thus, the response pattern is complex, and the authors attribute this change to local selection regime in the system: increased variation in precipitation leads to greater temporal and spatial variation in soil moisture conditions within the experimental plots. This drives differential selection in different parts of the experimental plots in a first step towards niche differentiation. Avolio et al. (2012) conclude that in populations where initial genetic variation is sufficiently high, increased climate variation can lead to increased local genetic differentiation via differential selection and ultimately to niche differentiation. Overall, however, genetic diversity will at best remain constant in the species as none of the above processes creates new genetic variants but rather favours local shifts of allele frequency and the persistence of immigrating alleles.

We argue that increasing climate variability can generally lead to changes in the selection regime that can cause either increases or decreases in local genetic diversity. Under conditions of increased temperature extremes or increased frequency of severe precipitation events, directional selection on dispersal traits could shift towards better dispersing capabilities to help populations avoid more frequent extreme weather conditions. This can change the distribution of genetic diversity by (i) decreasing effects of genetic drift by means of increased gene flow, thus homogenizing genetic diversity across space or (ii) increasing abundance of rare genotypes with particularly good dispersal abilities. However, empirical studies have shown that the relationship between habitat stability and dispersal is not clear-cut and that positive selection on dispersal abilities mainly occurs under conditions with predictable environmental changes (reviewed by Ronce 2007; see also Box 2). When conditions are unpredictable, mechanisms of reduced local competition and local extinction probabilities complicate the situation (Ronce 2007).

Increased climate variation can provide strong selection pressure on traits that are related to increased phenotypic plasticity as organisms need to adapt to a less predictable environment. In a study on phenotypic diversity in great tits (Parus major Linnaeus 1758), Nussey et al. (2005) show that there is selection towards increased plasticity regarding their breeding time. Phenotypic plasticity in breeding time is heritable, and phenotypes with low plasticity in breeding times are selected against because anthropogenic environmental change, including GCC, has led to phenological mismatches between the birds and their caterpillar food resources.

The effect of multiple anthropogenic stressors. While microevolutionary adaptation affects specific, functionally relevant parts of the genome, natural and anthropogenic stress, for example, parasites, environmental pollution, habitat perturbation or habitat fragmentation can also lead to unspecific reductions in effective population size by diminishing census population size, distorting sex ratios, reducing fecundity rates and increasing mortality (Lande 1988; Reed 2005) and thus additionally reducing genetic diversity by increased drift and inbreeding (Nowak et al. 2009). The impacts of stressors are generally augmented in situations where human habitat fragmentation limits gene flow among subpopulations (Frankham 1995; but see Cobben et al. 2011). Such multiple stressor conditions can initiate an extinction vortex (Gilpin & Soulé 1986; Fagan & Holmes 2006) where

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decreasing genetic diversity itself leads to decreased stress resistance. Ultimately, populations may become strongly inbred, causing dramatic increases in stress sensitivity and thus enhanced extinction risk. Although the effects discussed above are probably not a comprehensive account of all possible effects of GCC on genetic diversity, it is clear that the overall level of genetic diversity will likely drop in many populations and species affected by GCC even if their range and demography may appear unaltered (e.g. Yang et al. 2011).

How is the effect of GCC on genetic diversity currently studied?

The potential effects of GCC on species and both neutral and non-neutral genetic diversity have been studied at various scales albeit rarely as the explicit goal of the respective studies. Some studies have used range-wide or large-scale inferences of species historic responses to climate change (e.g. based on population genetic structure [Jay et al. 2012] or phylogeographic data and inferences [e.g. Bálint et al. 2011]) to indirectly infer potential future responses to GCC or dispersal potential under GCC. In a more direct approach, ancient DNA studies have inferred the genetic effects of relatively recent climate change during the Holocene or late Pleistocene on intraspecific genetic diversity (e.g. Magyari et al. 2011). Another focus has been placed on directly linking functional genetic diversity with local climate adaptation, albeit primarily in model species for which genome-level resources were readily available (e.g. Hancock et al. 2011 and Fournier-Level et al. 2011 for A. thaliana). Since the development and rapid proliferation of SDM, these have sometimes been integrated with genetic diversity data to examine historic species responses (e.g. Richards et al. 2007; Cordellier & Pfenninger 2009; Theissinger et al. 2011). Most work, however, has been focussed on experimental studies with economically relevant organisms or model species. We discuss these approaches in turn below.

Can the past inform the future?

Insights on historic range shifts and historic distributions of genetic diversity. Most phylogeographic studies that disentangle population history during the Pleistocene and through the Holocene warming implicitly reconstruct the fate of genetic diversity during a major GCC (Avise 1998). Phylogeographic data sets inform how species reacted to GCC in the past, for example, by providing information on routes and time frame of the (re)colonization of the present range, long-term migration barriers, location of hybrid or suture zones, location of refugia, and/or temporal niche conservatism (Schmitt 2007; Scoble & Lowe 2010). Dispersal and migration mechanisms, in particular, have been one focus of inference for historic GCC responses based on phylogeographic data (e.g. Taberlet et al. 1998; Hewitt 1999; Abbott et al. 2000; Pfenninger & Posada 2002; Schmitt 2007; Engelhardt et al. 2011). Intuitively, it is clear that sedentary species have a disadvantage compared to mobile species in tracking suitable habitat conditions under GCC by means of migration (Callaghan et al. 2004). However, this drawback may be at least partially set off by passive dispersal (e.g. Bilton et al. 2001) or rare long-distance dispersal events (Nathan 2006).

Another focus of phylogeographic inference has been on locating refugia. This is important for predicting species responses to GCC for two reasons. First, knowing the location of refugia is important for assessing the scale and tempo of past migrations and range shifts of species in response to past GCC (e.g. Birks & Willis 2008; Petit et al. 2008). For example, it is clear from fossil data that small populations of many plant species have survived in favourable microhabitats (microrefugia) embedded within large unsuitable areas during periods of rapid climate cooling. These acted as source populations during subsequent warming (Birks & Willis 2008; Feurdean et al. 2012). Second, locating refugia can help us characterize the distribution of genetic diversity through space and time (e.g. Hewitt 1996), in particular, because refugia are often associated with higher levels of genetic diversity (Petit & Hampe 2006). The comparison of refugia to expansion areas may thus give an indication of how long it takes to build up predisturbance levels of genetic diversity. The fact that expansion areas can in many cases still be distinguished from last glacial maximum (LGM) refugial areas by their relative lack of genetic diversity is not a very encouraging prospect for the effect of the range shifts to come. At smaller scales, landscape genetic or demographic inferences can be used to identify habitats acting as barriers or corridors of gene flow, habitat characteristics of source and sink populations and locations of increased adaptive potential (Scoble & Lowe 2010; Hoffmann & Sgrò 2011). All of these aspects can provide important insights into assessing species reactions to future GCC, for example, how likely a species is to reach its projected future habitat under GCC conditions based on its past and present dispersal dynamics. An overall assessment of the adaptive capacity may be gained by estimations of how conserved environmental niches are and where areas of increased genetic diversity and likely increased adaptive potential are located. It is thus recognized that information on historic GCC reactions can be used to help making predictions about species future reactions (MacDonald et al. 2008; de Bruyn et al. 2012).
and examples have been published for terrestrial snails (Depraz et al. 2008) or Arctic marine mammals (O’Corr-Crowe 2008).

Integrating phylogeography and palaeoecological data for improved inference. Inferences about potential future reactions can be improved when they are not based on phylogeographic data alone, but wherever possible also integrate palaeontological proxy data (Dawson et al. 2011; but see Box 1 for problems in palaeontological data arising through cryptic diversity). Petit et al. (2008) show that some tree species persisted through periods of rapid environmental change that may be comparable in timescale to expected GCC in the 21st century. Their molecular data provide insights on the population level processes, in particular founder effects, bottlenecks, and migration patterns of individual intraspecific lineages. These processes would not have been uncovered by fossil data alone. However, the possible extinction of 89 tree genera during the Pleistocene can only be recognized through integrating palaeontological data. The local extinction of trees in Europe suggests that while some species persisted under severe conditions in the climatically dynamic Pleistocene in Europe, for example, in Fennoscandian Nunataks (Parducci et al. 2012), most did not (Petit et al. 2008).

Besides mobility, the above study on glacial tree persistence (Petit et al. 2008) raises the importance of timescale of environmental change. Under the current rapid rates of GCC, migration responses inferred from phylogeographic data sets may need to be reassessed for shorter timescales (years to decades rather than decades to centuries or millennia; Callaghan et al. 2004). One issue is whether the selected molecular loci are sufficiently responsive to rapid climate change and whether genetic signals in the examined loci remain detectable over time (Parducci et al. 2012). However, there is also evidence for very rapid historic climate change (Van Meerbeeck et al. 2009), and it is debatable whether species are currently facing more rapid GCC than in the past (Hof et al. 2011b). Based on our current knowledge on population displacement rates observed from actual range shifts over the last few decades (Chen et al. 2011) or inferred from molecular data (e.g. Petit et al. 2008), many species are unlikely to migrate fast enough to successfully track their habitats (Petit et al. 2008; Bálint et al. 2011). Whether these species will increase their migration rates, disperse by rare stochastic long-distance dispersal events (Nathan 2006), persist in small populations in suitable microrefugia or respond through tolerance mechanisms remains to be seen.

Phylogeography and niche conservatism. Phylogeographic inference is also often used to assess temporal niche conservatism within species and whether or not populations or species adapted to past environmental change (Callaghan et al. 2004). Comparative phylogeographic studies have shown that responses to past GCC can vary dramatically between closely related taxa (e.g. marine gastropods: Marko 2004; land snails: Pfenninger et al. 2007) or between species with similar present-day habitat preferences and ecologies (e.g. montane aquatic insects: Lehrian et al. 2009, 2010; Theissinger et al. 2011, 2012). Responses seem to be individualistic and specific for each examined taxon, which is not a promising prospect concerning the transferability of results among species. In some cases, responses also seem to vary at the intraspecific level, for example, between ESUs within a nominal morphospecies (e.g. Pauls et al. 2006; Theissinger et al. 2011). Nonetheless, inferences based on the past allow studying rates of biodiversity response to climate change and ecological resilience of individual species to climate change (Willis et al. 2010). As we begin to take the niche into account in assessing potential impacts of GCC, it is becoming clear that ecological or functional niches are often not conserved the way we assume (e.g. Pfenninger et al. 2007; Engelhardt et al. 2011; Yang et al. 2011) and that plasticity, rapid adaptations or complex ecological interactions will greatly complicate projections of future GCC effects unless we better understand these factors. This is particularly true for assessments that integrate SDM based on climatic niche, as shown by studies of invasive species that often successfully invade regions with climatic niches different from their native range (Sax et al. 2007).

What can we learn from integrating species distributions and range projections?

Species distribution models are widely used to project future suitable conditions for species, albeit with some major underlying assumptions (niche conservatism, modelling of relevant variables, mostly ignoring species interactions), and methodological limitations depending on the approach used. We do not discuss these here, as they were recently reviewed by Araújo & Peterson (2012). Integrating evolutionary aspects bears great potential for inferences on the effects of GCC on biodiversity and predictions on species distributions (Hoffmann & Sgrò 2011). Scoble & Lowe (2010), for example, make a case for integrating intraspecific genetic diversity data in the form of phylogeographic and landscape genetic data into SDM. Several recent studies have implemented SDM and future predictions of climatically suitable ranges in neutral genetic diversity assessment of nonmodel organisms (Bálint et al. 2011 and Taubmann et al. 2011 for montane aquatic insects; Habel et al. 2011 for butterflies;
Sork et al. 2010 and Alsos et al. 2012 for plants). Three methodological issues are common to all these studies that were recently addressed by Pfenninger et al. (2012): Is the sampling of genetic variation sufficient to make reliable assessments on projected allele losses? Is the genetic diversity level that is assessed relevant for evolutionary processes? Is the scale of SDM projections suitable for the sampling density of genetic diversity estimates in the study? See Box 3 for a framework to address these issues.

**Box 3 What is the best level of genetic diversity and geographical scale for assessing GCC effects in my data set?**

While research on the impact of GCC on ecosystems and species is flourishing, a fundamental component of biodiversity—genetic variation—has not yet received its due attention in this regard. The studies that have attempted to consider cryptic diversity when investigated the impact of GCC share some common limitations that restrict their information potential. First, it is not clear at which genetic level assessments should take place (e.g. haplotypes, different groups of haplotypes) and whether the considered level of genetic variation has been sufficiently sampled in terms of diversity and spatial scale. Second, the resolution of modelling projections should be fitted to the level of genetic information and sampling that is being assessed (i.e. projections with high spatial resolution may be suitable for studies with a high-resolution sampling, while the resolution of projections should be comparably lower in cases where the sampling is coarse). Pfenninger et al. (2012) suggest a methodological framework for projecting the loss of intraspecific genetic diversity under GCC (Fig. 2). The approach makes use of existing techniques like hierarchical genetic clustering methods, species accumulation curves (SAC) and SDM. Their approach begins with assessing the appropriate level of genetic variation for projecting the impact of GCC on genetic diversity. The rationale here is that the highest resolution of intraspecific variation that can be sampled depends on the marker system used and that it is impossible to account for all genetic variants occurring in natural populations at this level. Additionally, an individual genotype or haplotype is likely to be irrelevant in evolutionary terms for populations and species. In contrast to individual genotypes and haplotypes, higher levels of intraspecific genetic variants [e.g. ESUs (Bálint et al. 2011), GMYC species (Monaghan et al. 2009) or hierarchically nested clade levels (Pfenninger et al. 2012)] (i) can be exhaustively sampled and (ii) most importantly are more likely to be relevant for the evolution of a population or species. The next step is to assess the completeness of genetic sampling at the chosen level of inference using SAC at the level of genetic units. The third step is to choose the appropriate scale of spatial inference for genetic diversity loss prediction. This is defined by the geographical resolution at which the sampling of the genetic diversity is comprehensive or complete and may be found by an iterative process that comprises using increasingly higher levels of genetic diversity, the resampling of the regions of interest, reducing the resolution of SDM projections or any combination of these. The final step is to make projections of range losses and associated losses of genetic diversity based on the genetic and geographical scales that have been sufficiently sampled (Fig. 2). The suggested approach presents a feasible method to tap the rich resources of existing phylogeographic data sets and guide the design and analysis of studies explicitly designed to estimate the impact of GCC on a currently still neglected level of biodiversity.

More generally, when making inferences about the future using SDM projections, we generally assume temporal niche conservatism. Callaghan et al. (2004) reviewed how estimations of current gene flow and species mobility compared with inferences about historic migrations or demographic changes can provide indications of the species ability to track their suitable habitats through time. For the pond snail *Radix balthica* (L., 1758), Cordellier & Pfenninger (2009) explicitly tested this assumption before projecting the species future potential range. The authors applied a model selection approach to infer the location of LGM refugia. Subsequently, they used environmental niche modelling and the species current distribution to assess temporal niche shifts. Their data supported climatic niche conservatism in *R. balthica*, allowing them to predict the potential future range of the species using forecasting SDM. Their analysis suggests that GCC will have an immense detrimental impact on the southern and central European populations of *R. balthica*.

*How are neutral and non-neutral genetic diversity linked to adaptive capacity under GCC?*

*Genetic diversity, phenotypic plasticity and local adaptation.* Toleration of changing GCC conditions or avoidance through habitat shift is dependent on sufficient levels of adaptive capacity or ecological plasticity in affected species or populations. There is an inherent link between the standing genetic variation in a population and their potential for adaptation, but this link is not well documented in the GCC literature. Recent studies on trout
Jensen et al. (2008) and butterflies (Fischer & Karl 2010) illustrate that information about life history trait responses along an environmental gradient or to changing climate conditions provides insight into the adaptive capacity of species by illustrating the degree of life history plasticity in a (meta)population’s gene pool. Genetic variation and adaptive potential across a species’ gene pool and adaptation can be important to help tolerate...
new conditions but also when selection acts on dispersal capabilities of species (Canale & Henry 2010). Ultimately, life history traits and resulting phenotypes are the factors that determine whether a species or population is able to cope with GCC, not neutral genetic variation (Callaghan et al. 2004). Thus, there is a great need to better understand the genomic basis for life history traits, their regulation and resulting phenotypes and their respective variation.

Phenotypic plasticity, that is, an individuals’ capacity to regulate its physiology to best cope with prevailing or changing environment conditions (Canale & Henry 2010) is an important mechanism for dealing with GCC. Details on phenotypic plasticity are poorly known for many groups of organisms, particularly for diverse biota that are difficult to work with experimentally, for example, many marine species (Hallegraeff 2010). Maximizing an individual’s ability to respond to changing environmental conditions comes at the cost of reducing energy inputs elsewhere, for example, reproduction (Canale & Henry 2010). Thus, there are limits to the potential phenotypic plasticity of individuals, populations and species. As a direct consequence, phenotypic plasticity should be highest in long-lived organisms as they cannot withstand high selective pressures, due to slow generation times (Canale & Henry 2010), and need to invest energy in reproduction less frequently than species with short generation times (Pianka 1970). Trees are an exception of long-lived organisms that can rapidly adapt to changing environmental conditions due to the immense effective population size, high genetic variation (even in individual trees) and great reproductive potential (Petit & Hampe 2006). Canale & Henry (2010) recently reviewed adaptive plasticity in vertebrates and conclude many species responses to GCC are linked to plasticity rather than genomic adaptation. This finding highlights the need for much more multiple scale ‘omics’ research, not only focussing on genomics, but also on transcriptomics and proteomics in our efforts in understanding species’ stress responses (Wullschleger et al. 2009). The results also show that besides detailed experimental studies examining ‘omic’ responses to GCC, the life history traits of a target species should be studied or at least evaluated before making predictions about species potential responses to GCC, although we recognize that this will probably remain feasible only for a fraction of organismal biodiversity. Yang et al. (2011) show, for example, that putative specialist species may be less specialized to the factors they were considered specialists for, but more specialized for other, previously ignored conditions (e.g. habitat vs. climate niche). Engelhardt et al. (2011) find evidence for a shift in dispersal behaviour of an aquatic insect. Wing length polymorphism observed in many other insect taxa has been linked to genetic controls (e.g. Westermann 1993), environmental cues (e.g. Aukema 1990) or a combination of both (e.g. Aukema 1990), suggesting that in some species dispersal capacity is highly plastic.

Increased efforts to combine basic autecological research with the study of adaptive and neutral genetic diversity (e.g. Brown & Paxton 2009; Angeloni et al. 2012) as well as future range projections as advocated by Dawson et al. (2011) to assess species vulnerability under GCC conditions will aid assessments of GCC impacts. Environmentally responsive plasticity (polyphenism) that is linked with genetic polymorphism between individuals may also be a first step in the evolutionary process (see Schwander & Leimar 2011 for a recent review). Thus, preserving (or losing) the varying degrees of plasticity within individual populations of a morphospecies has evolutionary implications as well.

Species with small ranges. Small-range species are considered more strongly threatened by GCC (Hering et al. 2009; Morueta-Holme et al. 2010) and provide another example where plasticity is very important to assess GCC impacts. Small-range species with low effective population size are more likely to have low genetic diversity and thus reduced adaptation potential, and small-range endemics of colder climates (high altitude or high latitude) may be locally adapted to colder climatic conditions. This makes them primary targets for conservation efforts (see Box 2), but the degrees to which most of these species are really climate sensitive remains unclear, because little is known about the ecological and phenotypic plasticity of most species.

Stress tolerance and gene expression. An increasing number of studies have examined links between intraspecific genetic variation and stress tolerance. Many studies link measures of neutral genotypic diversity with fitness parameters. For example, Procaccini et al. (2007) linked genotypic diversity with population growth and resilience to perturbation in seagrasses. Williams (2001) presented evidence that genetic diversity is linked to increased sexual reproduction and stronger vegetative propagation for eelgrass populations exposed to thermal stress. Using microsatellites, Nowak et al. (2009) show that chemically stressed midge populations significantly decrease their levels of neutral genetic diversity after only 12 generations resulting in a lowered fitness when exposed to a second stressor (Vogt et al. 2010). It has to be noted, however, that the theoretical basis underlying heterozygosity-fitness correlations (HFC; Hansson & Westerberg 2002) is not fully understood and remains debated (Szulkin et al. 2010). Models and empirical evidence indicate that inbreeding will only be reflected
in neutral diversity markers under certain conditions that are only met in endangered species with a recent population history involving strong inbreeding (Balloux et al. 2004; Slate et al. 2004; see also Box 2). More recent evidence, however, seems to support the suitability of commonly applied multilocus markers under the assumption of a certain degree of inbreeding in the respective population (Szulkin et al. 2010), but with high levels of uncertainty. Modern marker systems that allow genome-wide scans of genetic diversity will likely add to the understanding of commonly observed HFC and provide improved accuracy in estimations of inbreeding coefficients (Chapman et al. 2009).

More recently, studies have moved towards linking genetic diversity with responses in gene expression. Bahrndorff et al. (2010) examined heat shock resistance in isogenic lines of springtails and observed variations in expression of response genes, although they were unable to detect significant correlations between response gene expression and thermotolerance. While several studies have found genetically controlled changes in traits in response to stress, a direct link between neutral and non-neutral genetic diversity and concrete stress response is rarely found (Hoffmann & Daborn 2007), except of the observation that in small and genetically impoverished populations inbreeding depression is frequently enhanced under stressful environments and may enforce the extinction risk of populations (Armbruster & Reed 2005; Nowak et al. 2007). Measuring neutral genetic variation is still valuable because it is likely to complement adaptive capacity (Scoble & Lowe 2010) and because it reflects important aspects of genetic diversity (population dynamics and migration, drift, mutation) that are relevant for assessing the impact of GCC on genetic diversity patterns (Sgrò et al. 2011). It is, however, also clear, that there is a necessity to further examine non-neutral genetic diversity to better assess the adaptive capacity of populations (Kramer & Havens 2009) and gain a better mechanistic understanding of species responses to GCC.

Where is potential for future research?

Despite the wealth of studies dealing with the GCC on species distribution, the number of studies that incorporate genetic diversity is still quite limited. Above, we argued why GCC impact studies can become much more realistic and in many ways more relevant if they account for or integrate intraspecific genetic variation and effects on this variation. Here, we outline approaches and areas of research that we believe would further our understanding on the issue.

To date, most research on genetic impacts of GCC has focused on neutral genetic variation, either from a theoretical point of view (e.g. Arenas et al. 2012) or in empirical studies (e.g. Hallatschek et al. 2007; Pfenninger et al. 2011; Rubidge et al. 2012). This is mainly resulting from the ease and low cost of assessing this level of genetic diversity in nonmodel organisms. Microarrays, quantitative PCR (qPCR) and next-generation sequencing now also allow assessing climatically relevant loci (Reusch & Wood 2007). Genome scans using amplified fragment length polymorphisms (jump et al. 2006, 2008), SNP–based methods or differential display (Miyakawa et al. 2010) allow screening genome-wide diversity at both neutral and functional sites even for large-scale studies at a reasonable cost and effort (Davey et al. 2011). Such approaches are particularly effective for species with a sequenced genome (Hohenlohe et al. 2010; Tollrian & Leese 2010). Microsatellites are well established as population genetic markers and are reasonably easy and cheap to develop. Recent studies have shown that microsatellites can also indicate selective loci, for example, through hitchhiking selection of other candidate loci that can for example be detected screening of EST libraries (Nielsen et al. 2009). First pioneering studies in the GCC framework start to emerge using this technique on model species like A. thaliana (e.g. Fournier-Level et al. 2011; Hancock et al. 2011), but also nonmodel species like the butterfly Aricia agestis (Denis & Schiffermüller, 1775) (Buckley et al. 2012). These kinds of studies will ultimately allow scientists to assess the grade of current local adaptedness of populations to current climate conditions, which genes are responsible for adaptation to changing environmental conditions, and the genetic basis for phenotypic plasticity responses to GCC.

Making the functional link between particular candidate genes, their geographical distribution and their environmental relevance remains a complicated endeavour that is time-consuming, experimentally tricky and costly. In the foreseeable future, these approaches will primarily remain suitable only for a few taxa that are experimentally tractable. Transferability of results among taxa would make single taxon studies more relevant, but this remains to be tested. Thus, examining neutral genetic variation as a simple but rough proxy for adaptive variation is still relevant, and it is likely to remain so for years to come. However, with the recently introduced poolseq method (Futschik & Schlötterer 2010), population genomic approaches covering the entire genome have the potential to soon become commonplace far beyond model organisms (Fabian et al. 2012).

The use of putatively neutral genetic variation as a proxy would be even more valuable, if we had a quantitative overview of the link between (neutral) genetic variation and quantitative, selectively non-neutral variation and phenotypic or functional variation. The currently
available studies appear to suggest a relatively weak connection (Reed & Frankham 2001; Leinonen et al. 2008; Olano-Marin et al. 2011; Szulkin & David 2011). This relation is likely to vary among taxa due to variation in genome size or intron/exon ratios. A broad taxonomic overview, however, is currently still lacking. Similarly, establishing a functional link between the often shown correlation of (neutral) genetic diversity with population and individual stress resilience (e.g. Nowak et al. 2007) appears a rewarding issue, not only in the GCC debate. One way to integrate most of the above identified research approaches is the $Q_{ST}/F_{ST}$ framework (Whitlock 2008; Le Corre & Kremer 2012) that is currently rarely used in a GCC context, but see Frei et al. (2012) for an exception. However, not all taxa can be bred as required for this type of analysis. If the organism is at least experimentally tractable under common garden conditions, the $P_{ST}/F_{ST}$ framework (Brommer 2011) may provide an attractive alternative, in particular in conjunction with SNP-based genome scans (Edelaar et al. 2011). Using such an approach, Nemec et al. (2012) could show that variance in population growth rate as a response to exposure to different temperatures among populations of nonbiting midges (Chironomus riparius Meigen 1804) along a climatic gradient is partially explained by variance in genetic diversity. Otherwise, genome scans combined with association mapping (Holliday et al. 2010; Mariac et al. 2011) can be a feasible way to link candidate loci and phenotypic variation with environmental variation.

In current studies on the effects of GCC on genetic structure, spatial climatic gradients are often used as a surrogate for climate variation over time (Aratújo & Rahbek 2006). However, natural archives preserving DNA (Angeler 2007; Magyari et al. 2011), museum collections (Wandeler et al. 2007; Bálint et al. 2012; Rubidge et al. 2012) or monitoring programmes using cryobanking (Lermen et al. 2009) provide valuable and still underused resources for genetic material from time series and allow direct study of GCC-related genetic changes in populations and species over time. For other temporal changes of human-induced environmental conditions such archives have been successfully used to understand changes in the hybridization patterns of Daphnia spp. Müller, 1785 (Brede et al. 2009). Up to now, there are no published studies using biological archives to study climate-driven changes in the distribution of genetic diversity over time, but as we are aware of some ongoing projects, these are likely to appear in the near future.

Few studies to date have explicitly addressed the impacts of increased climate variation on the genetic diversity. The few studies that have, for example Avolio et al. (2012), show that the responses are relatively complex and that increased variation can have direct impacts on the selective regime of species. This can be related to dispersal, tolerance of extreme temperature or moisture conditions, or phenotypic plasticity but is not limited to these aspects. Experimental evolution studies [see Kawecki et al. (2012) for a recent review] hold the potential to address these aspects if short-term climate variation is incorporated into the experimental design. We expect that good experimental systems and particularly multigeneration studies will provide much insight into the interaction of climate change, climate variation and genetic diversity.

Dawson et al. (2011) propose an integrated approach to assessing impacts of GCC on biodiversity that integrates these aspects and focuses on species vulnerability under GCC conditions based on (i) a species’ sensitivity to climate change conditions, (ii) a species’ adaptive capacity and (iii) a species’ exposure to changing climate conditions. The authors propose making use of the rich palaeontological, ecological and evolutionary literature to assess adaptive capacity and sensitivity of species to changing climate conditions and using distribution modelling to assess their future exposure. Similarly, integrating knowledge from phylogeography and SDM has the potential to assess a species GCC vulnerability by addressing aspects on sensitivity (e.g. past migration, population structure), adaptive capacity (e.g. estimates of genetic lineages and neutral genetic variation) and exposure (SDM).

As outlined throughout this review, intraspecific diversity assessments can help inform current and past dispersal of species and populations and help implement more realistic dispersal scenarios in GCC studies. Hoffmann & Sgro (2011) summarize different GCC response models that highlight the importance of demographic factors on the adaptive responses of species. These are often linked to effective population sizes as surrogates for genetic variation and different modes of gene flow. Improvements on these models and applying these models to species with sufficient background data offer important research opportunities in GCC biodiversity assessments. Simulation studies that use different migration scenarios can help us understand the biases in genetic diversity projections that are implicit in species or population projections that account for migration. Jay et al. (2012) introduce an approach called ancestry distribution models to estimate the admixture coefficients from putatively neutral markers based on their correlation with spatial and environmental data. This approach allows making predictions about the future displacement of contact zones between populations. Such developments promise great improvements in forecasting population genetics of species and offer important complements to more traditional SDM-based approaches. Additional improvements on SDM relate to
the importance of climatic parameters vs. other ecological parameters for species distributions in general, implementing more realistic migration models and models of habitat heterogeneity and fragmentation (Cobben et al. 2011), accounting for life history and ecological traits of species (e.g. mode of inheritance, generation, Cobben et al. 2011), choosing the correct scale for modelling (Pfinninger et al. 2012; see also Box 3), assessing the potential of cumulative effects of multiple stressors in GCC projections (Hof et al. 2011a; Müller et al. 2012) and integrating species interaction networks to account for potential biotic multipliers of climate change (Araújo et al. 2011; Zarnetske et al. 2012). As both the SDM methodology and our understanding of non-neutral genetic responses to environmental conditions in general and GCC conditions in particular progress, it may become possible to incorporate local adaptation in GCC models and projections (Atkins & Travis 2010), thus realizing the link of GCC projections with assessments of functional genetic diversity and ecological genomics. Ultimately, these integrative approaches in particular promise to become exciting research avenues in climate change biology.

Conclusions

As it is the foundation of biodiversity, inclusion of intraspecific genetic diversity into climate change assessments is essential. To date, however, most studies on GCC impacts, particularly those making predictions about future species ranges under GCC conditions, are based on nominal morphospecies and ignore intraspecific genetic diversity. This is a fundamental shortcoming, as it is clear that the effects of GCC vary among populations. Evidence for this phenomenon comes from many different approaches including direct assessment of climate-adaptive genetic loci in geographical populations (Fournier-Level et al. 2011; Hancock et al. 2011), projections of future population genetic structure of genomewide genetic diversity (Jay et al. 2012), assessments of climate change responses of populations based on neutral genetic diversity (Sork et al. 2010; Yang et al. 2011) and assessment of biodiversity losses under GCC conditions (Balint et al. 2011; Alsos et al. 2012). Including genetic diversity into GCC studies promises much improved projections of species vulnerability and future distributions, particularly in species where detailed information on the adaptive level of GCC responses is lacking. This is currently the majority of nonmodel organisms and clearly highlights the importance of further empirical study to test the evolutionary potential of species, populations and genotypes (Hoffmann & Sgro 2011).

Besides potentially improving GCC projections, incorporating aspects on intraspecific genetic diversity into global change biology offers exciting new integrated research possibilities, particularly in the advent of affordable, widespread use of both neutral and functional genetic variation and the increasing availability of genomic resources for nonmodel organisms. Ultimately, the processes of GCC response can only be understood at this level, while studies of neutral genetic variation provide a framework for identifying species or population of particular importance and threat under GCC but cannot provide insight on the genetic response mechanisms to GCC. Finally, the integration of neutral and functional genetic diversity with a better understanding of the autecology of species, for example, from more experimental or observational studies, but also from indirect inferences like the ones outlined in this review from phylogeography, will provide clearer insights into short-term responses to GCC and provide the basis for predicting the responses of species to ongoing GCC.

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